Vocal repertoire of sooty mangabeys (*Cercocebus torquatus atys*) in the Taï National Park

Friederike Range¹ & Julia Fischer²

¹Department of Psychology, University of Pennsylvania, 3815 Walnut Street, Philadelphia, PA 19104, USA; range@cattell.psych.upenn.edu (corresponding author)
²Max-Planck Institute for evolutionary Anthropology, Inselstraße 22, 04103 Leipzig, Germany;

Short Title: Vocal repertoire of sooty mangabeys

Word Count: 5 667
Abstract

Recordings of sooty mangabeys (*Cercocebus torquatus atys*) in their natural environment were used to compile the vocal repertoire of this species. All calls are described according to their acoustic features and the behavioural context in which they occurred. Descriptions are supplemented by quantitative measurements of call occurrence of all age-sex classes. This study was designed to increase our understanding of the influence of phylogeny and habitat constraints on the acoustic features of vocalizations by filling the gap of our knowledge about vocalizations of terrestrial old world primates that live in dense rainforests.

Introduction

One important aspect in the study of the evolution of nonhuman primate vocal behaviour is to uncover the selective pressures that shape the structure of vocalizations and determine the repertoire morphology. Traditionally, repertoires have either been described as ‘graded’ or ‘discrete’, or a mixture of the two (Marler 1967, 1976). A graded signal system is characterized by continuous acoustic variation between and/or within signal types, with no obvious distinct boundaries that allow a listener to discriminate easily between one signal type and another. Discrete repertoires, on the other hand, contain signals with no intermediates between call types. Marler hypothesized that graded vocal repertoires should evolve when individuals inhabit relatively open habitat and interact at high rates and at close range with conspecifics. In contrast, discrete vocal repertoires should be favoured when auditory signals must operate without accompanying visual or other contextual cues; for example, in forest habitats or when being broadcast over long distances (Marler 1976). Marler also hypothesized that long-distance calls should be acoustically distinct because other cues may be lacking.
Most information about the structure of vocal repertoires has been collected either on savannah-dwelling old-world monkeys or arboreal new world monkeys or lemurs (e.g. Macedonia 1993; Schott 1975; Fischer & Hammerschmidt 2002; Cleveland & Snowdon 1982; Struhsaker 1967). However, to obtain a comprehensive understanding of the effects of phylogenetic descent and habitat on the acoustic structure of vocalizations, it is essential to accumulate information about related species living in habitats with different demands on the acoustical features of vocalizations. For example, compared to savannah dwelling monkeys, primates that live in forest habitats face the problem of sound transmission through dense vegetation. Several studies have shown that vocalizations used for defending territories or enhancing inter-group spacing have acoustical features that improve long-distance transmission through rain forest environments (e.g. cottontop and Geoffroy’s tamarins (Cleveland & Snowdon 1982); langurs (Horwich 1976); gibbons (Deputte 1982); mangabeys (Waser 1982). The dominant energy of these calls usually falls between 500 and 2500 Hz, frequencies that travel farther than higher frequency sounds (Marten & Marler 1977; Waser & Waser 1977)). In contrast to calls that are used for long-distance communication, calls used in within group communication typically are produced at higher frequencies and lower source levels.

Sooty Mangabeys (*Cercocebus torquatus atys*) are Old World monkeys that belong to the family cercopithecidae. Traditionally, all mangabeys have been combined into the single genus *Cercocebus* (Napier & Napier 1967) that was commonly divided into two species groups: the terrestrial torquatus-group and the arboreal albigena-group. However, recent studies suggest that these species-groups are paraphyletic (Barnicott & Hewett-Emmett 1972; Cronin & Sarich 1976; Disotell 1996; Fleagle & McGraw 1999) and should be placed in two separate genera. Accordingly, the torquatus-group, including sooty mangabeys, is assigned to the genus *Cercocebus*, which is most closely related with
mandrills and drills (Mandrillus), whereas the albigena-group belongs to the genus Lophocebus, which is most closely related to baboons (Papio) and geladas (Theropithecus).

Sooty mangabeys are terrestrial, forest-dwelling monkeys that live in large multi-male-multi-female groups. Considering their phylogenetic descent as well as the general features of sooty mangabey social organization and the dense vegetation in the Taï forest, where visibility ranges between 5-20 meters, sooty mangabeys constitute an interesting species to fill the gap of our knowledge about the acoustical structure of vocalizations of terrestrial Old World monkeys living in rainforests. We describe the acoustic features of the most frequent vocalizations given by different sex-age classes and examine the behavioural context in which specific call types are produced.

**Methods**

**Study site and subjects**

The study was carried out over a 16-month period (April 2000 – December 2001) on free-ranging sooty mangabeys in the Taï National Park in Ivory Coast (6° 20'N to 5°10'N and 4°20'W to 6°50°W). The park is the last remaining major block of primary forest in West Africa and covers approximately 454,000 ha. Visibility ranges from 5 to 20 meters throughout the home range of our study group.

During the study period, group size ranged between 98 and 122 animals. All animals were well habituated to human observers and recognized individually. The group has been under study since 1997.

**Data collection**

Behavioural data were collected by focal animal sampling (Altmann 1974). Focal samples were 15 minutes long with at least 60 minutes between consecutive samples of the same individual. During observations, we used instantaneous sampling (Altmann 1974) to record the activity (foraging,
travelling, social interaction or resting) and the position of the focal animal relative to others. Spatial positions were designated by the presence of other individuals in a circular area with a radius of 10 meters surrounding the focal animal. If there were other individuals on all sides, the focal was in the centre position (c), if other individuals were on only one side, the focal was considered to be in a border position (b), whereas if no other group member was within 10 meters, the focal was scored to be in the periphery (p). Social interactions and vocalizations were recorded continuously (for details of the ethogram see Range & Noe 2002).

Behavioural data were recorded by F. Range on adult females during the first study period (April – August 00) and on juveniles during the second study period (May – December 01). Y. Meystre collected behavioural data on adult males (October 00 – April 01).

All vocalizations were recorded opportunistically during the second study period (May – December 2001) using a Sony-DAT PCM-M1 recorder and a Sennheiser directional microphone (ME 68). Whenever a call was recorded, information regarding the caller’s identity, the behavioural context, and the identity of the neighbours within 5 meters was determined. Behavioural context was described as accurately as possible.

Data analysis

1. Behavioural analysis

Grunting time for each female was defined as the percentage of minutes during focal animal sampling when the focal individual grunted at least once. We used the Wilcoxon matched pair test to determine whether or not grunting was dependent on the spatial position of the focal animal within the group (center vs. periphery or border).
We calculated hourly rates of vocalizations for different sex and age classes by dividing the total number of calls heard during focal samples by the sum of the total observation time. Correlations between dominance rank and rate of vocalizations were calculated using the Spearman rank coefficient.

2. Acoustic analysis

To document the acoustic features of the sooty mangabey vocal repertoire we used only vocalizations tape-recorded from adult individuals. A total of 737 calls were analysed. All statistical analyses were performed on individual means.

Tape-recorded vocalizations of sooty mangabeys were categorized by ear. For those call types for which only a small number of examples were recorded, the spectrographic analysis was performed using Cool Edit (Syntrillium, Phoenix, AZ). We measured call duration, dominant frequency and the number of syllables for these calls.

Vocalization types for which sample size were large were submitted to the SIGNAL sound analysis system (Beeman, 1996) and a fast Fourier transform was conducted (grunts: 1024-pt FFT, time step: 3 ms, frequency resolution: 11 Hz; twitter: 1024-pt FFT, time step: 3 ms, frequency resolution: 46 Hz; alarm calls: 1024-pt FFT, time step: 5 ms, frequency resolution: 46 Hz). The resulting frequency time spectra were analysed with a custom software program, LMA 8.4 (Hammerschmidt 1990). The program extracts different call parameters that describe the acoustic structure of each call. For the present analysis we used the following two parameters:

1. Duration (ms): Time between the onset and end of a call.
2. Median of the first dominant frequency band (Hz): i.e. the median of the lowest dominant frequency band calculated across all time segments of a call.

We used Mann-Whitney-U tests to compare acoustic features in different contexts. The presented spectrograms were generated with Avisoft-SASLab.

Results

Grunts. Grunts are short vocalizations given in a variety of contexts (Figure 1). They were the most frequent vocalizations given by all members of the group. The mean (± SD) duration of female grunts was 119.67 ± 16.86 ms (N = 34). The median of the first dominant frequency band of grunts given by females had a mean (± SD) of 263.52 ± 59.34 Hz (N = 34).

Figure 1

Temporal structure

A clear variation in temporal structure of call bouts was observed between adult males and adult females. Adult males usually grunted several times in a row with regular intervals of about 186.58 ms between grunts (n = 5)(Figure 2), whereas inter-call intervals in female grunts ranged from a few seconds to a few minutes and varied between contexts.

In contrast to females, the overall rate that adult males grunted was negatively correlated with rank (Spearman rank correlation $r_s = -0.745; n = 11; p = 0.0084$) (Meystre 2002).

Figure 2
Behavioural context

Adult females:

1. Foraging: Adult females often grunted when they were feeding or searching for food. Usually, individuals gave several grunts with varying inter-call intervals from a few seconds up to several minutes. Focal females grunted significantly more often when they were in a border or peripheral position compared to situations when they were surrounded by other group members (Wilcoxon matched pairs test, n = 24 females, z = - 4.143, p<0.001).

2. Social grunts not involving infants: Adult females and juveniles often grunted when they approached or groomed another group member or when they were approached or groomed by another individual.

3. Social grunts involving infants: Females and juveniles often approached, grunted and embraced adult females with infants. In contrast to other grunts, individuals in this context always grunted several times with a short, regular inter-call interval and usually incorporated another vocalization, the twitter, into the sequence in this context.

4. Other: Grunts were also recorded when animals were travelling or sitting. However, small sample sizes limited testing if these grunts differed from grunts given during foraging or social interactions.

Grunts tape-recorded during social interactions (Figure 2B and 2C) such as approaching, embracing, grooming and infant handling differed significantly in the median dominant frequency band from grunts recorded during foraging (Figure 2A) but not in the mean grunt duration (Table 1).
Adult males:

1. Dominance interactions: Adult males often grunted after they approached or threatened a lower-ranking male and that male had reacted with submissive behaviour.

2. Male-female interaction: Adult females with sexual swellings often approached and presented their swellings to adult males, who inspected the swellings but then turned away. When the female left, the males usually grunted.

3. Foraging: Adult males occasionally grunted during foraging.

Due to small sample sizes no statistical analysis is available on the acoustic structure of grunts given by adult males.

Twitter. A mangabey twitter could sound soft and melodic or sometimes a bit harder, almost harsh (Figure 3). We currently don’t know if these acoustic differences are due to individuality or context. Twitters given by adult females during foraging and social interactions were always given as trains with up to 23 syllable (median = 5.6, n = 33). Mean duration (± SD) of syllables was 50.26 ± 6.60 ms (n = 33). Each syllable consisted of several, irregular modulated frequency bands ranging between 1 and 20 kHz. The mean (± SD) of the fundamental frequency band was 2026.68 ± 72.17 Hz (n = 33).
Twitters were only heard from adult females and juveniles of both sexes and usually given in similar behavioural contexts as grunts:

1. Foraging: Adult females as well as juveniles of both sexes frequently twittered when they were searching for food. Calls were often answered by other nearby animals either by emitting the same call type or by grunting (Figure 3A).

2. Handling infant: As described above, individuals often twittered in combination with grunts when they touched or handled an infant (Figure 3B).

3. Sitting between subgroups: During low-food availability, groups of sooty mangabeys are usually widely dispersed when foraging and distances between small groups of individuals can reach up to 100 meters. In these circumstances, adult females were often observed producing a certain type of twitter (Figure 3C+D). Typically, this vocalization was accompanied by the signaller looking towards the direction of another subgroup. As soon as a subgroup would approach the other, the vocalizing female would stop calling and join the other animals.

No significant difference was found between the acoustical structure of twitters given during foraging and twitters given when handling an infant regarding the number of syllables per call or the median of the first frequency band (Table 2). However, the duration of syllables was significantly longer during foraging compared to the duration of syllables given in social interactions (Table 2).

Agonistic Vocalizations

Screams. Screams are noisy vocalizations produced only in agonistic interactions. The duration of screams emitted by adult females ranged in length from 0.22 to 3.121 seconds (mean = 1.35 s; n = 25). They were comprised of both tonal and harsh elements. The tonal structure – fundamental with several accompanying overtones – was often overlaid with wide-band noise up to 15 kHz. The intensity of this
noise differed between calls so that in some calls the harmonic structure was not visible at all (Figure 4A). In other calls, harmonic structure became visible in the beginning of a scream (Figure 4B) or appeared occasionally throughout the call (Figure 4C).

Figure 4

Most screams were recorded from juvenile animals and adult females. Even though conflicts between adult males were frequent, adult males rarely screamed. Screaming of adult and juvenile animals occurred in two sub-categories of aggressive interactions.

1. Screams occurred during contact aggression when, after a conflict, the aggressor took the tail of the loser into its mouth. During the tail bite, the loser crouched to the ground, screamed and often defecated (Figure 4A). Screaming in this context was observed in all sex-age classes but rarely in adult males. Overall rates were rather low for adult females (0.04 h⁻¹) and slightly higher for juveniles (0.09 h⁻¹).

2. Individuals frequently screamed when they themselves were attacked but redirected the aggression towards the aggressor. Most frequently, this behaviour was observed of juveniles challenging either other juveniles or adult females (0.34 h⁻¹). Adult females often screamed when they directed aggression towards adult or sub-adult males (Figure 4B und C), but also when attacking other females or juveniles (0.03 h⁻¹). Only once we tape-recorded an adult male screaming at another group member - an adult male (Figure 4D). The screaming of individuals in this behavioural category often resulted in agonistic support from nearby animals.
Due to small sample size, we could not test whether the amount of bandwidth (noise) in a scream was correlated with different patterns of agonistic interactions.

In contrast to older animals, infants screamed in a wide variety of behavioural contexts. They were also observed to give screams that occurred in combination with harsh twitters when the mother neglected or rejected their attempts to drink or to be carried as well as when alarm calls occurred (Figure 4E).

**Growl.** All tape-recorded growls were comprised of several acoustically similar syllables that were sometimes combined with other call types (see below). Each growl syllable consisted of a low fundamental frequency band with several accompanying overtones (Figure 5A+B). The fundamental frequency for adult female growls was 236.36 ± 171.89 Hz (mean ± SD; n = 11). The upper limit of the total energy of these calls ranged from 1000 to 11500 Hz for individual females (mean ± SD = 4436.36 ± 2917.28 Hz; n = 11).

Individuals of all sex/age classes used this vocalization in agonistic interactions with other group members. Typically, the higher-ranking individual in a conflict raised its eyebrows, stared and growled at the opponent. Often, the aggressor would alternate this behavioural sequence with rapid turns of its head towards other high-ranking individuals, which often resulted in agonistic support.
Other threat vocalizations

Four other vocalizations were recorded during agonistic interactions of group members. Three different calls were heard in combination with growls during the same type of agonistic interaction as described above. The “grumble” lasted between 266 to 482 ms and had a fundamental frequency between 100 and 200 Hz (n = 3) Figure 6A). Two other calls (Figure 6B and C) were recorded only a few times during agonistic encounters. The first, a “hoo” call, occurred between growl syllables and had a rich harmonic structure. The latter call was very similar to the twitter given by adult females sitting between subgroups and alarm calls and occurred mainly in intense conflicts.

The last call type, “wau” was heard five times during the entire study and was recorded only once (Figure 6D). Adult males that watched an intense fight between other adult male members of the group emitted the call.

Copulation call. Only females emitted these calls, and only when they had a sexual swelling. The mean duration (± SD) of copulation calls was 7.47 ± 2.24 seconds (n = 21). Copulation calls were given as phrases with up to 31 syllables (median = 15; n = 21). Usually, calls of individual females were compromised of two tonal syllable types with different acoustical structures (Figure 7).
In Taï, sooty mangabeys exhibited a distinct mating season. Females emitted these calls mainly during copulations. Males usually did not vocalize during copulation, but sometimes grumbled after ejaculation.

**Long call (Whoop Gobble).** All long calls started with an introductory note, which could be separated from the rest of the call by up to 4.45 seconds (Figure 8). After that, the call was comprised of one or two types of tonal syllables. The first type was a long, frequency modulated syllable with a frequency bandwidth of about 1200 Hz. The second type was much shorter, showed less frequency modulation and had several harmonics reaching frequencies up to 5200 Hz (n = 5). While the first syllable type was present in all analysed calls the second type was only present in two calls from two different males. All long calls ended with a frequency-modulated call that had several harmonics. The endnote was again separated from the main part of the call by several hundred milliseconds.

Figure 8

Long calls were given exclusively by adult males. The males would usually call several times and often alternate long calls with alarm calls (see below). Long calls were often heard in the morning or when another mangabey group was nearby. The call was also sometimes heard in combination with sightings or actual attacks of predators.

**Alarm calls.** Alarm calls of adult females had a median duration of 383.33 ms and were significantly shorter than alarm calls emitted by adult males, which had a median duration of 641.05 ms (Mann-Whitney U= 19.50; n₁ = 21; n₂ = 7; p<0.01). Moreover, the median of the first dominant
frequency band was significantly higher in alarm calls given by adult females (2189 Hz) than in alarm calls given by adult males (1573.67 Hz) (Mann-Whitney U = 5.00; n₁ = 21; n₂ = 7; p < 0.001).

Sooty mangabeys gave alarm calls mainly towards three different predators: snakes, eagles and leopards.

1. Snakes: Sooty mangabeys have only been observed to react towards Gabon vipers (Bitis gabonica). These snakes were found regularly (2-3 times per week) by group members and always elicited alarm calls. Upon hearing the alarm calls, other mangabeys approached the vocalizing animal, climbed 1 or 2 meters up into a tree and scanned the forest floor for the viper.

2. Eagles: One of the main predators of sooty mangabeys in Taï is the crowned eagle (Shultz & Noë, 2000; Shultz, 2001). Although actual predation attempts were observed infrequently (3 times in 6 months), the eagle was detected at least 4 or 5 times per week perching up in a tree or flying over the canopy close to the group eliciting alarm calls by mangabeys.

3. Leopard: Leopards have been observed to attack members of our observation group several times. Typically, sooty mangabeys jumped up into a tree upon hearing or seeing a leopard and gave alarm calls.
We found no significant difference in duration or median of the first dominant frequency band between male alarm calls given in three different contexts: eagle, group encounter and leopard (Kruskal-Wallis Test; H = 2.424; df = 2; p > 0.05 and Kruskal-Wallis Test; H = 0.157; df = 2; p > 0.05). Alarm calls given by adult females in different contexts – eagle, viper and leopard – differed significantly in duration (Kruskal-Wallis Test; H = 8.272; df = 2; p < 0.05) but not in the median of the first dominant frequency band (Kruskal-Wallis Test; H = 3.047; df = 2; p > 0.05).

Discussion

The sooty mangabey vocal repertoire consists of nineteen vocalizations that differed from each other either in their acoustical structure or in the behavioural context with which they were associated. The number of audibly distinct calls given by sooty mangabeys is similar to the number of audibly distinct call types given by other primate species (e.g. baboons (*Papio* spec.): 15 (Rowell & Hinde 1962); *Macaca fuscata*: 37 (Itani 1963); *Cercopithecus aethiops*: 36 (Struhsaker 1967); *Pan troglodytes*: 25 (Goodall 1965)). However, it is likely that we missed some rare vocalizations due to the limited scope of this study, and that the vocal repertoire of sooty mangabeys will have to be revised over time.

With respect to acoustic features that improve sound transmission through dense vegetation, all long distance vocalizations were compatible with our expectations and had their strongest energy within the frequency range of 500 to 2500 Hz.

Sooty mangabeys use close-range vocalizations that seem very similar to vocalizations used by savannah dwelling species (e.g. vervets and baboons). Acoustic analyses of grunts that were tape-recorded in a variety of behavioural contexts showed differences in the acoustical structure of grunts
given in foraging and social contexts as has been demonstrated for other primate species (e.g. savannah baboons (Cheney & Seyfarth 1982; Rendall et al. 1999). A more detailed acoustical analysis of mangabey grunts will test whether these differences persist if we control for individuality and whether more specific behavioural contexts can be distinguished. In contrast to grunts, twitters given by adult mangabey females and juveniles are remarkably different from vocalizations emitted by savannah-dwelling old-world monkeys, but are similar to vocalizations given by arboreal new-world monkeys (e.g. *Samiri sciureus* (Winter et al. 1969)).

The comparison of the acoustical structure of vocalizations between species is particularly interesting in regard to the factors that underlie repertoire morphology (Fischer & Hammerschmidt, 2002). It has been theorized that the acoustic structure of vocalizations is determined by the call’s functions (Marler 1965; Marler 1967). If vocalizations are used over long distances, they should be discrete to reduce ambiguity between call types, whereas vocalizations that are emitted during face-to-face interactions can be more graded since other cues – visual and olfactory - are available to help the receiver determine the signal’s meaning. However, some recent studies also showed that these predictions are not always met. The Barbary macaques’ alarm calls, for instance, form an acoustic continuum despite significant variation in relation to the stimulus that elicited the calling (Fischer et al. 1995). Even more puzzling, baboon alarm calls grade into their contact and contest calls (Fischer et al. 2001; 2002).

Several playback experiments have demonstrated, however, that although human observers describe certain close-range calls as graded signals, monkeys perceive these calls in a more discrete manner and react differently according to small differences in the acoustic structure (e.g. Cheney & Seyfarth 1982; Rendall et al. 1999; Fischer 1998; Fischer et al. 2001b). Moreover, although alarm calls can be acoustically discrete from each other, they also can grade into other, close range vocalizations that are
used in social contexts. For example, vervet snake alarm calls can easily be discriminated from vervet eagle or leopard alarm calls, but they grade into chutters that are used in vervet close-range vocal communication (Struhsaker 1967; Cheney 1984).

Sooty mangabeys are terrestrial, and most social interactions occur when individuals face each other. According to the theory (Marler 1965; 1967), we expected that calls given in these situations would be acoustically graded. Grunts, twitters, growls and screams seem to be acoustically discrete, but gradations occur within call types.

In contrast to these close-range vocalizations, we would have expected alarm calls and calls that are used to communicate between subgroups or neighbouring groups to be more discrete. Considering the spectrograms of twitters, intermediate forms of twitters given in different contexts seem likely. Moreover, twitters seem to grade acoustically into snake and possibly leopard alarm calls. Furthermore, male alarm calls given in response to different predators did not differ in acoustical structure from each other. This last result was probably due in part to high within-male variation in the acoustical structures of alarm calls, and in part to the ambiguity of situations in the field. For example, even though we heard a neighbouring group nearby, the tape-recorded alarm call might have been given in response to an eagle that was not detected by the observer. However, if only contextual ambiguity were responsible for this effect, no variation in acoustical features of alarm calls by adult females would have been expected. We did, however, find that at least duration differed significantly between alarm calls given towards different predators. A larger sample size of alarm calls from known adult males and carefully designed playback experiments will help to elucidate this question.

In accordance with other studies on vocalizations of non-human primates, it seems that several factors such as body size, phylogenetic descent, social structure and probably habitat may be important in shaping a species’ repertoire (Hohmann & Herzog 1985; Hauser 1993; Hammerschmidt & Fischer
Our study shows that sooty mangabeys use both vocalizations reported for savannah dwelling old world species and vocalizations used by arboreal new world species. Moreover, acoustic gradations seem to occur between and within call types, a result, puzzling especially in regard to long-range vocalizations and the functional hypothesis about the evolution of graded versus discrete vocalizations. However, play back experiments have yet to be conducted to examine whether mangabeys recode the graded variation in vocalizations into discrete meaningful units.

Acknowledgments

We thank the Ministère de la Recherche Scientifique and the Ministère de l'Agriculture et des Ressources Animales of Côte d'Ivoire for permission to conduct our research in the Taï National Park. We are grateful to the CSRS and the staff of the CRE research station in Taï for logistical support. F.R. was supported by the "DAAD Doktorandenstipendium im Rahmen des gemeinsamen Hochschulsonderprogramms III von Bund und Laendern". Richard Peho and Gerard Gha provided invaluable assistance in the field by locating the study group and by collecting data. We than, the members of the Taï Monkey Project for support in the field and R.Noë, R. Seyfarth, D. Kitchen and J. Crawford for comments on earlier drafts of the manuscript.

References


Legends

Figure 1: Representative grunts from one female sooty mangabeys in three different contexts. A) Foraging; B) Social, not involving an infant; C) Social, involving an infant.

Figure 2: A) Male grunting bout. B) One grunt from the same male.

Figure 3: A) Twitter of a foraging adult female. B) Twitter of an adult female handling an infant. C) and D) Twitters from two adult females sitting between two subgroups.

Figure 4: A) Adult female screaming after tail bite from another, higher ranking female. B) Adult female screaming at a sub-adult male C) Adult female screaming at an adult male D) Adult male screaming at another adult male. E) Infant chuttering and then screaming at its mother who resists the attempts of her infant to nurse.

Figure 5: A) Adult female growling. B) Third syllable of the first call.

Figure 6: A) Adult female grumbling. B) Call element recorded during growling of a 5 year old male. C) Call elements recorded during growling of juvenile female. D) “Wau” call of adult male.

Figure 7: Copulation call of an adult female with maximum sexual swelling.

Figure 8: Loud call (Whoop gobble) of the alpha male. I-Note = Introductory Note. E – Note = Endnote.


Table 1: Parameters that were analysed to detect differences in the acoustic structure of grunts and twitters between contexts. Contextual differences were tested with the Mann-Whitney U test.
Figure 1
Figure 2
Figure 3
Figure 4

Figure 5
Figure 6
Figure 7

Figure 8
Figure 9
Table 1

<table>
<thead>
<tr>
<th>Vocalization</th>
<th>Context</th>
<th>Social Mean</th>
<th>Social n</th>
<th>Foraging Mean</th>
<th>Foraging n</th>
<th>U</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Median</td>
<td>n</td>
<td>Median</td>
<td>n</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>dominant</td>
<td></td>
<td>frequency</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>frequency</td>
<td></td>
<td>[Hz]</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Grunts (Adult females)</strong></td>
<td></td>
<td>282.92</td>
<td>26</td>
<td>226.16</td>
<td>31</td>
<td>240.00</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>Duration [Ms]</td>
<td>114.9</td>
<td>26</td>
<td>116.5</td>
<td>31</td>
<td>383.50</td>
<td>Ns</td>
</tr>
<tr>
<td><strong>Twitters (Adult females)</strong></td>
<td></td>
<td>7.51</td>
<td>24</td>
<td>5.27</td>
<td>22</td>
<td>193.5</td>
<td>Ns</td>
</tr>
<tr>
<td></td>
<td>Syllables per call</td>
<td>1997.31</td>
<td>24</td>
<td>2053.34</td>
<td>22</td>
<td>218.00</td>
<td>Ns</td>
</tr>
<tr>
<td></td>
<td>Median dominant frequency of</td>
<td>35.38</td>
<td>24</td>
<td>60.8313</td>
<td>22</td>
<td>123.00</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>syllables [Hz]</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Duration of syllables [Ms]</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*p < 0.05, **p < 0.01